

# THE MYRMECOPHILOUS PTINIDAE (COLEOPTERA), WITH A KEY TO AUSTRALIAN SPECIES

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## ABSTRACT

A review is presented of the current knowledge on ptinid beetles known to occur with ants. Included are: 1) a catalogue of the myrmecophilous Ptinidae, 2) a summary of biological and distributional data, 3) a revision of the genera and key to the species occurring in Australia, and 4) a discussion of the origin and evolution of myrmecophily in the family. Eight genera and 43 species are treated, and 8 previously recognized genera are placed into synonymy. A list of ant host species is also given.

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## INTRODUCTION

The family Ptinidae includes about 50 genera and 600 species, which are distributed throughout the major regions of the world but are particularly abundant in the drier parts of the subtropical and temperate zones. Of the described species, almost 50 have been recorded from the nests of ants and at least 42 appear to be true inquilines. The purposes of this paper are (1) to propose certain changes in the classification of the myrmecophilous species on the basis of newly discovered characters, (2) to provide a key to the species occurring in Australia, (3) to summarize what is presently known about the biology and distribution of myrmecophilous ptinids in the form of a catalogue, and (4) to speculate on the possible origin and evolution of myrmecophily in the family.

Those species of Ptinidae which are here considered to be true ant guests fall into five main groups: the two tropical American genera *Gnostus* and *Fabrasia*, the South African *Diplocotidus*, the southeast Asian genus *Myrmecoptinus*, and the several Australian genera which have usually been placed in the subfamily Ectrephinae. The first four of these will be discussed briefly below and the last will be treated in detail in a later section.

In addition to the above, several ptinids have been recorded from the nests of ants. The European *Ptinus subpilosus* Sturm and *P. sexpunctatus* Panzer have been taken with the ants *Acanthomyops fuliginosus*

(Latreille) and *A. brunneus* (Latreille); both beetles occur in other habitats as well (Linsley, 1944; Howe, 1959). The species *Diplocotidus moseri* Brauns was described from specimens collected under a rock with the ant *Meranoplus peringueyi* Emery in South Africa (Wasmann and Brauns, 1925). Andreae (*in litt.*) has examined the type and considers it to be an old and rubbed specimen of *Pseudomezium coquereli* (Fairmaire). This record with ants is probably accidental. Finally, the species *Leioptinus inflatus* Wasmann (1928) was described from a nest of *Myrmicaria arachnoides* Smith on Sumatra. This species may be myrmecophilous, but from the description and illustration it does not appear to us to belong in the family Ptinidae.

*Gnostus* and *Fabrasia*.—These two genera, which contain all of the New World myrmecophiles, have been treated elsewhere (Lawrence and Reichardt, 1966a) and will not be discussed in detail here. Since the publication of the above revision, however, two new records have come to our attention. A specimen of *Fabrasia borgmeieri* Lawrence and Reichardt, in the collection of the Departamento de Zoologia, was collected at Poços de Caldas, Minas Gerais, Brazil, in February, 1933, with the ant *Camponotus (Myrmobrachys) senex* (F. Smith). This represents a southern range extension and a new species of ant host. A specimen of *F. wheeleri* Lawrence and Reichardt, in the collection of the California Insect Survey, was collected 6.3 miles west of Tehuantepec, Oaxaca, Mexico, on July 21, 1952, by E. E. Gilbert and C. D. MacNeill (ant host not recorded). This is the first record of *Fabrasia* from Mexico and represents a considerable northern range extension for *F. wheeleri*, known previously from Colombia.

*Diplocotidus*.—With the removal of *D. moseri* (see above), this genus contains a single species, *D. formicola* Peringuey, which occurs in the interior of South Africa. Andreae (*in litt.*) considers these to be true myrmecophiles and has seen two unde-

scribed species from the same area. The species differs considerably from other myrmecophilous ptinids and probably represents an independent line. The construction of the prothorax (Fig. 29), the subquadrate and concave clypeus (Fig. 3), and the aedeagus with reduced parameres (Figs. 26, 27) are all unique. The grooves on the pronotum are somewhat similar to those of *P. coquereli* and some of the South African gibbiines, but the species does not appear to be closely related to any of these.

*Myrmecoptinus*.—*Myrmecoptinus butteli* Wasmann (1916) was described from Sumatra and associated with the ant *Crematogaster butteli* Forel. Although Wasmann's type has not been examined, several specimens have been seen from Ceylon, Borneo, China, North Vietnam, and Burma that conform fairly well with the description and probably belong in the same group. The elytral humeri are well developed, the wings are present, the clypeus is flattened and triangular like that in *Ptinus* (Fig. 2), and antennal modifications are completely absent. The pronotum is relatively simple but has a well-defined, narrow, transverse groove at the base, which connects lateral pairs of processes resembling the trichomes found in other inquilines. The color is black and the vestiture is sparse, consisting of fine hairs as in other myrmecophilous forms. One of the specimens examined was collected by Mjöberg in an ant nest, but the locality is indecipherable. These beetles are probably myrmecophiles, but they do not appear to be closely related to the other groups.

Ectrephinae.—The majority of myrmecophilous Ptinidae occur in Australia and are generally placed in the subfamily Ectrephinae. These will be discussed further below.

#### Notes on Terminology

There are a few terms used in the key and discussions that may need clarification, although the usage is essentially the same

as that found in Lawrence and Reichardt (1966a).

*Clypeus.* This is equivalent to the area referred to by Stickney (1923) as the post-clypeus. In most Ptinidae it consists of a well-defined, broad, triangular plate lying just in front of and between the antennal fossae, the anatomical base of the plate forming the apex of the triangle (Fig. 2). The word "apex" in the text refers to the anatomical apex to which the labrum is attached. Many of the myrmecophilous species have a more elongate and tumid clypeus (Figs. 1, 4, 7, 8), while in several others it consists of a flattened, cleft plate (Figs. 5, 6, 9, 10).

*Trichomes.* In the supplement to Torre-Bueno's *Glossary of Entomology* (Tulloch, 1960), trichomes are defined as "modified hairs present on certain myrmecophilous insects which give off secretions which ants imbibe." Although the word may be used to describe any group of hairs which are thought to be glandular, it is commonly restricted to distinct setiferous processes usually found on the prothorax, antennae, elytra, or abdomen of myrmecophilous beetles. Actually, statements about the function of these structures are seldom, if ever, accompanied by histological or behavioral studies (see p. 12).

In the Ptinidae there are four main kinds of structures which may be glandular: (1) elytral pores, (2) femoral trichomes, (3) pronotal trichomes, and (4) antennal pilosity. The first two structures are found only in the genus *Fabrasia*; the elytral pores secrete a white waxlike substance. In some ptinids, such as *Ectrephes formicarum* Pascoe (Fig. 28) and *Enasiba tristis* Olliff, the pronotal trichomes bear distinct pubescence and resemble those occurring in the Paussidae (Darlington, 1950). Many species, however, have lateral clefts and processes (Figs. 30-32, 34) that appear to be homologous to the trichomes of *E. formicarum* but that do not bear patches of hairs. One feature that all of these structures share is the proximity of the tips of

two processes arising on different sides of a cleft or fovea. Perhaps this is a device for collecting a drop of liquid. In the following discussions all of these prothoracic structures are called trichomes. Patches of short hairs or pile are usually found on the last antennal segment (Figs. 17-19), and in some species they are concealed within a concavity at the tip of the segment (Figs. 15, 16). Occasionally the hairs may be absent (or rubbed off), but the extremely fine punctation may indicate the presence of a glandular area (Fig. 22).

*Measurements.* The total length is the maximum length as measured from above (tips of elytra to the most anterior point of the clypeus). EL and EW refer to greatest elytral length and greatest elytral width, respectively.

#### CLASSIFICATION OF MYRMECOPHILES

The placement of myrmecophiles in a system of classification has always presented a problem to taxonomists because of the development in these forms of special adaptations associated with inquilinous habits. In some groups normally conservative characters, such as the number or shape of antennal segments, may be highly variable, while in others entirely new structures, such as trichomes, may be present. It is not surprising that a number of these species have been placed in separate families until more careful studies have clarified their relationships. A few of the many beetle families originally proposed for the inclusion of inquilines but no longer recognized are the Pseudomorphidae (Carabidae), Clavigeridae (Pselaphidae), Rhysopaussidae (Tenebrionidae), and Cosysphodidae (Tenebrionidae).

During the last hundred years there has been considerable difference of opinion as to the placement of the myrmecophilous ptinids within the higher classification of the Coleoptera. Although Westwood (1855) considered *Gnostus* to be related to the Xylophaga of Latreille, later workers placed it near the Paussidae, Pselaphidae,

or Scydmaenidae; the taxonomic history of the genus is discussed by Lawrence and Reichardt (1966a). Pascoe (1866) compared his genus *Ectrephes* with *Gnostus* and the Paussidae. Gemminger and Harold (1869) proposed the family Gnostidae to include both *Gnostus* and *Ectrephes*, while Wasmann (1894) proposed the family Ectrephidae for *Ectrephes* and Westwood's two genera *Diplocotes* and *Polyplocotes*. Sharp and Muir (1912) noted the similarities between *Polyplocotes* and *Ptinus* with respect to the basal connection of the lateral and median lobes of the aedeagus. In 1916, both Wasmann and Mjöberg treated the ectrephines as members of the Ptinidae. Forbes (1926) pointed out the relationship of *Gnostus* to the ptinids on the basis of wing venation, but the complete absence of wings in the ectrephines made a similar comparison impossible. Our studies definitely confirm the inclusion of this group within the Ptinidae. *Diplocotes familiaris* (Olliff), one of the least specialized of the Australian species, differs little from other wingless ptinids, and a gradation can be seen from *D. familiaris* to the highly modified forms discussed below. The aedeagi of *D. familiaris* (Fig. 23), *D. laticornis* (Lea) (Fig. 24), and *Ectrephes formicarum* Pascoe (Fig. 25) all have the same basic structure found in *Gnostus* and *Fabrasia* (Lawrence and Reichardt, 1966a) and in various other ptinids (Hinton, 1941).

Within the Ptinidae, the classification of these myrmecophilous species presents a problem, owing to the present need for a complete revision of the family. Two subgroups, the Gibbiinae and the Ptininae, are usually recognized. In the former, the elytra are laterally compressed and partly enclose the reduced abdomen; the group includes *Gibbium*, *Mezium*, *Damarus*, and a few other genera, the species of which are most abundant in South Africa. The remainder of the ptinids are usually included in the Ptininae, which contains a diverse assemblage of forms.

The inclusion of various myrmecophilous

species in the family has led to the proposal of several more subfamilies. The genus *Ectrephes* Pascoe, along with Westwood's genera *Diplocotes* and *Polyplocotes* and Olliff's *Enasiba* and *Diphobia*, was placed in the Ectrephinae, while *Gnostus* was placed in the Gnostinae. Mjöberg (1916) divided the ectrephines into three subfamilies: Polyplocotinae, containing most of the species; Paussoptininae, for those species with flattened antennal segments; and Ectrephinae, including those species originally placed in *Ectrephes*. He placed *Diphobia* and the South African genus *Diplocotidus* Peringuey in the subfamily Ptininae, because of the lack of antennal modifications. Martinez and Viana (1965) proposed the name Fabrasinae for the genus *Fabrasia*, and Costa Lima (1962) placed his genus *Plaumanniola* in the Plaumanniolinae. The latter genus was found to belong to the family Scydmaenidae (Lawrence and Reichardt, 1966b).

We are of the opinion that there are at least five independent stocks of myrmecophilous ptinids: *Gnostus*, *Fabrasia*, *Diplocotidus*, *Myrmecoptinus*, and the ectrephines. The last group may be divided into two subgroups (see below), but their derivation from a single ancestor is indicated by the numerous parallelisms displayed by the two. *Myrmecoptinus* differs only slightly from the ptinines and could hardly be placed in a separate subfamily. *Gnostus* and *Fabrasia*, on the other hand, are quite distinct, although they are derivable from some of the more elongate and parallel-sided winged Ptininae. *Diplocotidus* is also a very distinct form and might well be placed in a separate subfamily, for which a new name would be required. The Ectrephinae are linked with the Ptininae by forms like *D. familiaris*, and the only character which could be used to distinguish the two groups is the form of the clypeus, which is elongate and tumid or cleft in *Diplocotes* and its relatives. If subfamilies or tribes are recognized, then, four would be required: one for each of the

Neotropical groups, one for the South African *Diplocotidus*, and one for the Australian ectrephines.

The second problem is whether or not these myrmecophilous forms are different enough from other ptinids to be placed in separate groups and what rank to assign to these groups. Within the large subfamily Ptininae, there are several other clusters of genera which are just as distinct, or more so, if one disregards the special adaptations of myrmecophiles. These include: *Diegous* and *Xylodes* from Mauritius; *Casopus* and its relatives from the Canary Islands; *Cylindroptinus* and its relatives from Southeast Asia; *Niptus* and its allies; *Sphaericus*; and *Trigonogenius*. Until a thorough study is made of the generic classification in the family Ptinidae, we think it serves no useful purpose to place the inquilinous species in separate subfamilies or tribes.

#### THE AUSTRALIAN ECTREPHINES

The 35 described species of myrmecophilous ptinids inhabiting Australia are generally placed within 14 genera, which are characterized mainly on the basis of antennal segmentation. *Diphobia* Olliff contains species with relatively simple, 11-segmented antennae (Fig. 21). Those species in which the penultimate antennal segment is enlarged (Figs. 17, 18) are placed in three genera according to the total number of antennal segments: *Diplocotes* Westwood (11), *Decemplocotes* Mjöberg (10), and *Polyplocotes* Westwood (9). In the monotypic *Hexaplocotes* Lea, the antennae are 6-segmented and the last two segments are enlarged and flattened (Fig. 22). In several species the antennal segments are strongly compressed and may be partially or completely fused to form a club (Figs. 19, 20); these forms have been placed in *Paussoptinus* Lea (10 segments; see p. 9), *Leaptinus* Mjöberg (10 segments), *Paussoceros* Mjöberg (9 segments), *Pseudectrephes* Pic (7 segments), *Monectrephes* Mjöberg (3 segments; see p. 10), and *Mesectrephes* Mjöberg (3 segments).

In *Ectrephes* Pascoe the antennae are 3-segmented and the last segment forms a solid, cylindrical club (Fig. 15), while in *Bitrephes* Oke they are 2-segmented and the terminal segment is somewhat wedge-shaped (Fig. 35). Finally, in the genus *Enasiba* Olliff the antennal segments are peculiarly shaped, as in Figure 16, and the pronotum is elongate, with four trichomes.

We feel that the above classification is unnatural for several reasons. First, any classification which relies so heavily on a single character complex is suspect. Furthermore, the particular characters used are highly variable within the group and are associated with a narrow specialization; thus they would have a low taxonomic weight according to the tenets originally proposed by Darwin. The adaptive nature of the antennal modifications becomes obvious if one considers the numerous cases of convergence with respect to these characters in unrelated myrmecophilous groups. The short, stump-like antenna of *Ectrephes formicarum* (Fig. 15), for instance, is very similar to that of *Gnostus*, and the same type of antenna may be found in several unrelated myrmecophiles, such as *Euclarkia* (Colydiidae), *Trochoideus* (Endomychiidae), *Fustiger* (Pselaphidae), and *Paussus* (Paussidae). Another objection is the lack of correlation of antennal characters with other features; *Diplocotes armicollis*, *Paussoptinus laticornis*, and *Mesectrephes kingi*, for instance, have very different antennal types and yet are similar with respect to the pronotum and clypeus. A further criticism may be made of the use of meristic characters (number of antennal segments), which should be given low weight for obvious reasons. The independent loss or fusion of antennal segments has been demonstrated in a number of beetle groups (Chapin, 1965, for the Coccinellidae; Lawrence, 1967, for the Ciidae), and extreme parallel reductions in myrmecophilous beetles have been discussed by Darlington (1950) for the Paussidae and Park (1942) for the Pselaphidae.

In an attempt to find other characters to use in classifying these Australian species, a study was made of the clypeal region. This structure had been ignored in the past because most of the specimens were glued to cards. In most Ptinidae the clypeus is broadly triangular and somewhat flattened, and the labrum is small and transverse (Fig. 2). With the exception of *Myrmecoptinus butteli*, all of the myrmecophilous species have the clypeus somewhat modified. The Australian forms fall into two distinct groups on the basis of clypeal structure. In the first group (Figs. 1, 4, 7, 8), the clypeus is slightly to strongly tumid and subtriangular, with the median portion, at least, distinctly punctate. In the second group (Figs. 5, 6, 9, 10), the clypeus is elevated, flattened, and deeply cleft at the apex, forming a U-shaped clypeal plate, which is impunctate and shiny. The species included in each group are given below according to their present generic assignments:

Group I: *Diphobia familiaris*, *D. foveata*, *D. intricata*, *D. longicornis*, *D. metallica*, *D. myrmecophila*, *Diplocotes armicollis*, *D. foveicollis*, *D. howittanus*, *D. minuta*, *Decemplocotes brevipeennis*,\* *D. strigicollis*, *Polyplacotes apicalis*, *P. carinaticeps*, *P. pilosus*,\* *P. similis*, *Paussoptinus laticornis*, *Mesectrephes kingi*, and *Bitrephes cuneiformis*.

Group II: *Polyplacotes castaneus*, *P. longicollis*, *P. longipes*, *P. nitidus*, *P. ovipennis*, *P. perforatus*, *P. scabricollis*,\* *Hexaplocotes sulcifrons*, *Leaptinus dolichognathus*, *Paussoceros antennalis*,\* *P. cremastogastri*, *Pseudectrephes clavatus*,\* *Monectrephes pascoei*, *Ectrephes formicarum*, *Eusasiba tristis*, and *E. microcera*.

The types of those species marked with an asterisk have not been examined, but in every case the descriptions, illustrations, or comparisons with known species have been sufficient to place the species with a reasonable degree of certainty in one group or the other.

Since the first type of clypeus is the most

easily derivable from that occurring in most Ptinidae and since the simplest type of antenna also occurs in the first group, it is reasonable to assume that this clypeal type is primitive. The joint possession of a relatively complex and derived clypeus by members of group II and the occurrence within each group of characteristic antennal and pronotal types present strong evidence that the division is a natural one. The parallel development of certain antennal modifications in the two groups is not surprising for myrmecophiles and would tend to support the ultimate derivation of both stocks from a common ancestor.

Within group I, it is difficult to segregate the species further without using too many generic names. If the antennae are used, five genera might be recognized, when meristic differences are ignored in the group characterized by having an enlarged penultimate antennal segment. In the structure of the prothorax, *D. armicollis*, *P. laticornis*, *P. carinaticeps*, *M. kingi*, and *B. cuneiformis* are similar (Figs. 30 and 35), but *D. foveicollis* is intermediate in this respect between these species and the remainder of group I. The clypeus of *P. carinaticeps* (Fig. 7) is unique in that it forms a narrow, median ridge, but that of *M. kingi* (Fig. 8) might well represent an intermediate condition. We think the most practical solution would be to consider all of the species in group I as belonging to a single genus, the oldest name for which is *Diplocotes* Westwood.

Within group II, there are at least three distinct subgroups. The genus *Eusasiba* is readily distinguishable on the basis of pronotal and antennal structure (Fig. 16). *Ectrephes formicarum*, *Monectrephes pascoei*, and *Pseudectrephes clavatus* may be united on the basis of pronotal structure; the pronotum has sharp lateral edges and the trichomes are lateral and similar in form (Fig. 28). *Ectrephes* is the oldest name for this genus. The remaining species do not vary considerably with respect to pronotal and antennal characters and are all in-

cluded in the genus *Polyplacotes* Westwood.

Although the generic classification presented here represents an improvement over the older classification, further modification may still be needed. When more species or character complexes are studied, it may be necessary to further subdivide the genera. A key to the genera and species of ectrephines is included below, followed by a brief discussion of each genus as it is here delimited. A résumé of the proposed classification, with generic and specific synonymies, is given in a later section.

### Key to the Genera and Species of Myrmecophilous Ptinidae Occurring in Australia

1. Clypeus usually subtriangular (Figs. 1, 4), slightly to strongly tumid, occasionally elevated, forming a narrow, median ridge (Figs. 7, 8) (genus *Diplocotes* Westwood) ..... 2
  - Clypeus elevated, flattened, and deeply cleft at apex, forming a U-shaped clypeal plate (Figs. 5, 6, 9, 10) ..... 20
2. Antennae 11-segmented ..... 3
  - Antennae with less than 11 segments ..... 12
3. Antennal segment 10 not enlarged, shorter than segment 11 (Fig. 21) ..... 4
  - Antennal segment 10 enlarged, longer than segment 11 and usually as long as segments 8 and 9 combined (Fig. 17) ..... 9
4. Antennal segment 11 very long, as long as segments 8 to 10 combined ..... *D. longicornis* (Lea)
  - Antennal segment 11 not as long as segments 8 to 10 combined ..... 5
5. Pronotum without basolateral trichomes, occasionally with weak lateral foveae ..... 6
  - Pronotum with distinct basolateral trichomes and deep lateral foveae ..... 7
6. Elytra shorter and broader, EL/EW less than 1.25, dark metallic blue in color, the punctation not distinctly seriate, each puncture rounded and bearing a relatively long, suberect hair ..... *D. metallicus* (Lea)
  - Elytra longer and narrower, EL/EW more than 1.25, reddish brown in color, the punctation distinctly seriate, each puncture elongate and bearing a very short, decumbent hair ..... *D. myrmecophilus* (Lea)
7. Antennal segments 6–10 shorter than broad, compressed, each segment bearing at the apex 4 brushes of yellow hairs ..... *D. intricatus* (Lea)
  - Antennal segments 6–10 as long as or longer than broad, not compressed, and without brushes of yellow hairs ..... 8
8. Elytral punctures very small and shallow, scarcely visible under lower magnification; pronotum without basomesal fovea ..... *D. familiaris* (Olliff)
  - Elytral punctures larger and more deeply impressed; pronotum with basomesal fovea ..... *D. foveatus* (Lea)
9. Pronotum expanded apically forming 2 lateral projections ..... 10
  - Pronotum without apicolateral projections ..... 11
10. Pronotum about as long as wide at base, apicolateral projection consisting of a sharp tooth; elytral punctures bearing very short, decumbent hairs ..... *D. armicollis* Lea
  - Pronotum more than 1.25 × as long as wide at base, apicolateral projection consisting of a rounded process bearing several small tubercles; elytral punctures bearing relatively long, suberect hairs ..... *D. foveicollis* Olliff
11. Total length more than 1.50 mm; basal impression of pronotum not expanded in middle ..... *D. howittanus* Westwood
  - Total length less than 1.25 mm; basal impression of pronotum slightly expanded in middle forming a shallow fovea ..... *D. minutus* Oke
12. Antennae 10-segmented ..... 13
  - Antennae with less than 10 segments ..... 15
13. Antennal segments 2–10 strongly compressed (Fig. 19) ..... *D. laticornis* (Lea)
  - Antennal segments 2–10 not compressed ..... 14
14. Pronotum with basolateral trichomes ..... *D. brevipennis* (Pic)
  - Pronotum without basolateral trichomes ..... *D. strigicollis* Lea
15. Antennae 9-segmented ..... 16
  - Antennae with less than 9 segments ..... 19
16. Clypeus elevated in middle, forming a narrow ridge (Fig. 7); pronotum shorter than wide at base, with apicolateral teeth ..... *D. carinaticeps* (Oke)
  - Clypeus somewhat tumid, but not forming a narrow ridge (Fig. 8); pronotum more than 1.20 × as long as wide at base, without apicolateral teeth ..... 17
17. Antennal segment 9 longer than 8 ..... *D. apicalis* (Oke)
  - Antennal segment 8 longer than 9 ..... 18
18. Total length less than 2.50 mm; elytral punctures bearing very short, decumbent hairs ..... *D. similis* (Oke)
  - Total length more than 2.50 mm; elytral punctures bearing relatively long, suberect hairs ..... *D. pilosus* (Mjöberg)

19. Antennae with 3 segments, the last segment strongly compressed .....  
     ..... *D. kingi* (Westwood) 21  
 — Antennae with 2 segments, the last segment wedge-shaped (Fig. 35) .....  
     ..... *D. cuneiformis* (Oke) 21
20. Pronotum with a narrow, median, longitudinal groove, and with 2 lateral and 2 mesal trichomes within a transverse basal impression; antennal segments 2 and 3 broadly joined, segments 3-5 somewhat triangular or wedge-shaped with the base broader than the apex, and segments 6-10 somewhat compressed (Fig. 16) (genus *Enasiba* Olliff) ..... 21  
 — Pronotum without a median, longitudinal groove, without trichomes or with only 2 lateral ones ..... 22
21. Head, pronotum, and bases of elytra bearing short, stout bristles, which are less than  $3 \times$  as long as wide; remainder of elytra bearing very short and fine hairs, which are barely visible under lower magnification; antennal segments 3-5 only slightly broader at base than at apex ..... *E. microcera* Clark  
 — Head, pronotum, and elytra bearing longer and finer bristles, which are about  $8 \times$  as long as wide; antennal segments 3-5 much broader at base than at apex .....  
     ..... *E. tristis* Olliff
22. Pronotum without lateral margins (Figs. 33, 34) (genus *Polyplacotes* Westwood) ..... 23  
 — Pronotum with sharp lateral margins (Fig. 28) (genus *Ectrephes* Pascoe) ..... 33
23. Antennae 10-segmented, segments 3-10 compressed ..... *P. dolichognathus* (Lea) 24  
 — Antennae with less than 10 segments ..... 24
24. Antennae 6-segmented, with the last 2 segments enlarged and compressed (Fig. 22) ..... *P. sulcifrons* (Lea) 25  
 — Antennae 9-segmented ..... 25
25. Antennal segments 3-9 compressed ..... 26  
 — Antennal segments 8 and 9 or none of them compressed ..... 27
26. Total length more than 2.50 mm; 9th antennal segment buried within the apex of the 8th ..... *P. antennalis* (Mjöberg)  
 — Total length less than 2.50 mm; 9th antennal segment not buried within the apex of 8th ..... *P. cremastogastri* (Lea)
27. Pronotum without basolateral trichomes or a basal impression; mesal portion of pronotal disc strigose (Fig. 33); clypeal plate with a lateral perforation beneath it ..... *P. perforatus* Lea  
 — Pronotum with basolateral trichomes; if basal impression absent, then mesal portion of pronotal disc not strigose; clypeus without perforation ..... 28
28. Pronotum without basal impression; mesal portion of pronotal disc not longitudinally strigose ..... *P. nitidus* Westwood  
 — Pronotum with basal impression; mesal portion of pronotal disc longitudinally strigose, at least basally (Fig. 34) ..... 29
29. Antennal segment 3 almost  $3 \times$  as long as wide ..... *P. longipes* Lea  
 — Antennal segment 3 not more than  $1.50 \times$  as long as wide ..... 30
30. Highest portion of pronotal disc very finely and sparsely punctate and shiny; anterior edge of pronotum with a transverse row of deep punctures (Fig. 34) .....  
     ..... *P. longicollis* Westwood  
 — Highest portion of pronotal disc more coarsely and densely punctate, granulate, or strigose, not shiny; anterior edge of pronotum without row of deep punctures ..... 31
31. Elytral punctation dual, with series of smaller and larger punctures .....  
     ..... *P. castaneus* Lea  
 — Elytral punctation not dual ..... 32
32. Antennal segments 4-7 slightly compressed, segment 8 distinctly compressed; total length 2.25 mm; Northern Territory ..... *P. scabricollis* Lea  
 — Antennal segments 4-7 moniliform, segment 8 only slightly compressed; total length 3 mm; South Australia .....  
     ..... *P. ovipennis* Lea
33. Pronotum without median fovea near the base (Fig. 28); antennae 3-segmented, the last segment forming a solid, cylindrical club without any trace of sutures (Fig. 15) ..... *E. formicarum* Pascoe  
 — Pronotum with median fovea near the base; antennae 7-segmented, or 3-segmented with the last segment flattened (Fig. 20) ..... 34
34. Antennae 7-segmented, the last 5 segments not fused together ..... *E. clavatus* Mjöberg  
 — Antennae 3-segmented with the club flattened and apparently consisting of 5 fused segments (Fig. 20) ..... *E. pascoei* Westwood

### Notes on the Genera

*Diplocotes*.—In most of the species, the clypeus is simple and only slightly convex (Fig. 1), but in others it is more tumid and may have a short carina above (Fig. 4). In *kingi* (Fig. 8) it is somewhat constricted in the middle, and in *cariniceps* (Fig. 7) a narrow, median ridge is formed.

The antennae may have from two to eleven segments. The simplest or least modified type of antenna occurs in *famil-*



*iaris* (Fig. 21); there are 11 segments, most of which are longer than wide, and the last segment is not modified at the apex. In *foveatus*, *longicornis*, *metallicus*, and *myrmecophilus*, the antennae are also 11-segmented, but the segments tend to be shorter and the last segment is truncate and pubescent at the apex. In *longicornis* the last segment is very long, and in *intricatus* most of the segments are transverse and several have apical pubescence. In several other species, the penultimate segment is enlarged and longer than the last segment (Fig. 17); these forms may have 11-segmented (*armicollis*, *foveicollis*, *howittanus*, and *minutus*), 10-segmented (*strigicollis* and *brevipennis*), or 9-segmented (*similis*, *apicalis*, *pilosus*, and *carinaticeps*) antennae. In *kingi* the antennae are 3-segmented, and the last segment is enlarged and strongly flattened, while *cuneiformis* has 2-segmented antennae with the second segment wedge-shaped (Fig. 35). *D. laticornis* presents a problem, since there has been some confusion concerning the number of segments in the antenna. There are apparently 10 segments, and the last nine are strongly flattened (Fig. 19). Mjöberg (1916) states that there are 11 segments and that segment 2 is greatly reduced, as in some species of Paussidae (see Darlington, 1950). After examining carefully the antenna of this species, we cannot agree with Mjöberg on this matter; the apparent second segment is actually a condyle attached to the real segment 2. It is more probable that reduction of segments has taken place at the apex of the antenna.

The simplest type of pronotum in this genus also occurs in *familiaris* (Fig. 32); a transverse, basal impression is present, anterolateral teeth and a median fovea are absent, and trichomes are small and indistinct. Other species may have various combinations of the above characters; *D. strigicollis*, for instance, has sharp anterolateral teeth on the pronotum but lacks a median fovea and trichomes, while in *D. longicornis* (Fig. 31) the teeth are lacking, but the

fovea and trichomes are quite distinct. In several species (*brevipennis*, *armicollis*, *laticornis*, *kingi*, *cuneiformis*, and *carinaticeps*), the pronotum is short and broad, with sharp anterior teeth, a median fovea, and distinct trichomes that are connected with longitudinal grooves on the disc (Figs. 30 and 35). *D. foveicollis* has a similar pronotum, but it is not as short and broad, and the anterior teeth are replaced by tuberculate processes.

The elytra in almost all of the species are bulbous and strongly convex, but in *D. myrmecophilus* they are somewhat flattened. In some species there may be several distinct pits at the bases of the elytra, but these are absent in *foveicollis*, *armicollis*, *laticornis*, *kingi*, *cuneiformis*, and *carinaticeps*.

*Polyplocotes*.—The clypeal structure in this genus does not vary considerably, but the shape of the clypeal plate and the extent of the apical cleft differ among the species. In *P. perforatus* there is a lateral perforation beneath the clypeal plate.

The antennae are less variable than in *Diplocotes*, and in most of the species they are 9-segmented with the penultimate segment enlarged (Fig. 18). In *P. longipes* most of the antennal segments are elongate, but in *longicollis*, *nitidus* and several others they are more robust and the last two are somewhat flattened. The antennae of *sulcifrons* (Fig. 22) are very similar, but there are only six segments. In *P. dolichognathus*, *P. antennalis*, and *P. cremastogastri* most of the antennal segments are flattened, as in *Diplocotes laticornis* (Fig. 19); in the first species the antennae are 10-segmented, while *antennalis* and *cremastogastri* have 9-segmented antennae.

Most of the species have a simple type of pronotum with a weak basal impression and small trichomes usually not visible from above (Fig. 34). In *P. perforatus* (Fig. 33) the basal impression is absent and the pronotum is narrowed anteriorly; basolateral trichomes are absent, but there are tufts of yellow hairs along the anterior

edge of the pronotum that may represent lateral trichomes that have been displaced.

*Ectrephes*.—The species in this genus fall into two groups: *E. formicarum* with a simple pronotal disc (Fig. 28) and the terminal segment of the 3-segmented antenna forming a solid, cylindrical club (Fig. 15), and the other two species (*pascoei* and *clavatus*) with a foveate pronotum and the distal antennal segments strongly flattened and variously fused so that the total number of segments is three (Fig. 20) or seven. It is interesting that these species and also *D. kingi* and *D. cuneiformis* have the tibiae enlarged and angulate proximally.

In the past there has been some confusion concerning the names *Ectrephes* and *Monectrephes*. Mjöberg (1916) divided *Ectrephes* into three genera: the original genus *Ectrephes* with its type *E. formicarum* Pascoe, *Mesectrephes* for *E. kingi* Westwood, and *Monectrephes* for *E. pascoei* Westwood. He also described another species, *E. clavatus*, which he referred to *Monectrephes*. Then in discussions of the various genera he continually transposed the names. He mentions that *Ectrephes* is the least differentiated, having the last segments of the antennae more or less joined together and the penultimate segment excavated at the apex and receiving the last (this is a description of *E. pascoei*, not *E. formicarum*). He then states that in *Monectrephes* there are only three joints, the last one being very long and forming a solid club (this refers to *E. formicarum*). This type of transposition occurs in several other places, including the key to the genera. Because of this, later authors (Lea, 1917; Pic, 1929) synonymized *Monectrephes* with *Ectrephes*, assuming that both were based on the same species, *E. formicarum*. In Mjöberg's first discussion of the genera, however, *E. formicarum* was referred to as the type of *Ectrephes* and *E. pascoei* was definitely placed in *Monectrephes*. The latter species is designated as type of *Monectrephes* in the catalogue below. We

think that Mjöberg had not misidentified the species but had merely transposed the names. If this hypothesis is acceptable, then *Ectrephes* and *Monectrephes* are based on different species and are not objective synonyms, although they are here considered to be subjective synonyms.

## ORIGIN AND EVOLUTION OF MYRMECOPHILY IN THE PTINIDAE

### Habitats and Food Habits

Most ptinid beetles are scavengers, and they are known to feed on a wide variety of animal and plant substances. The major kinds of habitats from which ptinids have been recorded are: (1) under bark and in decomposing wood, (2) in caves, (3) in the nests of birds and mammals, (4) in the nests of other insects, and (5) in association with various stored products of man. Because of the economic importance of these beetles, there have been several attempts to summarize the information pertaining to their biology; most of the following discussion is based on papers of Hinton (1941), Linsley (1944), and Howe (1959), all of which contain extensive bibliographies.

In Europe, *Ptinus subpilosus* Sturm, *P. palliatus* Perris, and *P. lichenum* Marsham are commonly collected under bark and in decaying wood. According to Crowson (1962), *P. subpilosus* occurs chiefly on old, mossy, partly dead oaks in Scotland, and the larvae have been found in decaying oak wood. The larva of *P. lichenum* has been reported to bore into dry fig wood (Howe, 1959), but no ptinid is known to utilize wood as food. Reitter (1911) records *P. subpilosus* from dry moss, *P. pilosus* Müller from old deciduous trees, and *P. sexpunctatus* Panzer from beneath pine and maple bark, and Linsley (1944) lists four other records from European literature. In North America, two species of *Ptinus* were collected by beating live oaks in southern California (Fall, 1901), a specimen of *P. bimaculatus* Melsheimer was taken in Spanish moss in Louisiana, and specimens of *P. fur* Linnaeus have been found in associa-

tion with *Pinus* in New England. Although the beetles may be feeding on rotten wood, it is also possible that they utilize insect remains or other organic debris.

Several ptinids have been recorded from caves, where they usually feed on bat guano or other mammal excrement. Brown (1959) described *Pseudeurostus kelleri* and *Niptus abditus* from specimens taken in caves in Utah, and four other species have been collected in caves in Europe and northern Africa (Howe, 1959). An undescribed *Niptus* was found feeding on raccoon scat in a Texas cave (Reddell, 1966). Although mammal dung appears to be an important food source in all the more sheltered habitats mentioned here, ptinid beetles have never been found in cattle droppings and are rarely collected in other kinds of dung in open places. One notable exception is given by Andrews (1967), who collected two Central American *Ptinus* in coati (*Nasua narica*) scat on exposed surfaces in a dry tropical forest.

The most important natural habitats of the Ptinidae are the nests of mammals, birds, bees, wasps, and ants. Linsley (1944) and Howe (1959) list 11 species of ptinids from mammal nests, 17 species from bird nests, and 12 species from the nests of hymenopterous insects. The actual type of food utilized varies with the kind of nest, but here again excrement is probably an important food item, along with dead insects, hair or feathers, pollen, and possibly living larvae. According to Linsley and MacSwain (1941), *Ptinus californicus* Pic, which lives in the nests of *Osmia*, does not attack the bee larva but may cause its death indirectly through competition for pollen. *P. sexpunctatus*, on the other hand, feeds on healthy larvae of *P. fur* (Howe, 1959). A number of economically important species, including *Niptus hololeucus* (Faldermann), commonly feed on rat and mouse feces, and the infestation of warehouses and mills by these beetles may be associated with the presence of rodents.

The biology of ptinids attacking stored

products has been adequately covered by Howe and others. Hinton (1941) lists 21 economically important species, and Howe (1959) has made detailed studies of 14 of these. Some of the many items on which ptinids have been reported to feed are: wheat, flour, rye, cereals, bread, hay, corn, ginger, nutmeg, cacao, opium, fish meal, sugar, pepper, tallow, wool, tobacco, paste, dried mushrooms, dried fruits, rubber, leather, plant and insect collections, and books. Although some of these records are suspect, the total range of food items is still very great.

### Biology of the Myrmecophilous Species

Very little is known about the habits of inquiline ptinids, and the present discussion is based partly on knowledge of the food habits of non-myrmecophilous species, facts concerning the distributions and nesting habits of host ants, interpretation of structural adaptations in the myrmecophilous Ptinidae, and information on the behavior of other myrmecophiles which have evolved analogous structural features.

Most, if not all, of the myrmecophilous ptinids would be considered symphiles or true guests, according to the ecological classification proposed by Wasmann (1898). Most of the species have the characteristic "symphilic features" mentioned by Donisthorpe (1927), Wheeler (1928), and Park (1964): smooth and shiny, black or reddish integument, reduced mouthparts, trichomes, and antennal modifications. Behavioral observations indicate that some species, at least, are tolerated and even protected by the ant colony. Clark (1923) noted that specimens of *Enasiba tristis* and *E. conifer* in an observation nest containing an active colony of *Iridomyrmex conifer* "seemed to be on friendly terms with the ants, and, during the three months' confinement were never interfered with, but were allowed to move freely through the various chambers, including the nurseries which always contained a large number of larvae and pupae of the ants." He further observed that "one,

and sometimes two ants were seen to attach themselves to the antennae, and appeared to be getting great satisfaction by nibbling and licking the apical joints, stroking the beetle meanwhile with their antennae. None of the ants were seen to attach themselves to the fascicles on the prothorax." The following comments were made about *Diplocotidus formicola* by Wasmann and Brauns (1925): "The species is not only tolerated by the ants but seems to be treated as a true guest like most of the Paussidae. When opening the ants' nest I have often observed that the *Plagiolepis* [*Anoplolepis* spp.] grasped the beetles and carried them away into security. . . . The behavior of the beetle is unconcerned. It runs carelessly in the thickest throng of the otherwise vicious and carnivorous *Plagiolepis* and can be observed sitting in copula in the crowd of ants." Although there is no other direct evidence pertaining to the biology of myrmecophilous ptinids, studies of other inquilinous beetles may shed some light on certain features, such as the functions of trichomes and antennal modifications, feeding and means of dispersal.

The tufts of hairs or trichomes on the prothorax, elytra, or abdomen of myrmecophiles secrete some substance which is imbibed by ants. The licking of trichomes by ants has been observed for a number of beetle groups, including the "lomechusine" Staphylinidae (Wasmann, 1920; Wheeler, 1928), the clavigerine Pselaphidae (Donisthorpe, 1927; Park, 1964), and the Paussidae (Reichensperger, 1948). In a detailed anatomical and histological study, Mou (1938) demonstrated that the trichomes of the Paussidae are definitely glandular, producing a secretion which evaporates slowly, leaving a greasy residue which is difficult to dissolve in alcohol but easily soluble in ethyl acetate. Park (1964) made the following comment on the behavior of ants which had been feeding on clavigerine trichomes: ". . . on several occasions, I have observed the workers to be so overwhelmed by this trichome stimu-

lant that they become temporarily disoriented and less sure of their footing." The predaceous reduviid bug *Ptilocerus ochraceus* Montandon produces a secretion which not only attracts ants but narcotizes them as well, enabling the bug to penetrate and feed on the paralyzed prey (Wheeler, 1928; Donisthorpe, 1927).

According to Wheeler (1928) the modified antennae of some myrmecophiles are adapted to stroking the ant host, or function as handles for the ants to carry the beetles about in the nests. According to Mou (1938) and Janssens (1949), however, the antennae of paussids are definitely glandular and probably serve the same function as the trichomes on the prothorax. The observations on *Enasiba* mentioned above indicate that this is also true in some Ptinidae. Darlington (1950) stresses the apparent loss of the tactile function in paussid antennae, as suggested by the reduction or loss of the pedicel and the associated Johnston's organ.

Since most other ptinids are scavengers, it is unlikely that the inquilinous forms feed on ant larvae as do staphylinids and paussids. The most probable sources of food are excrement, dead ants, and the remains of prey. In some of the Ptinidae, however, the mouthparts are reduced, indicating that they may be fed regurgitated food by the ants. Free-living ptinids, such as *Ptinus fur* (Figs. 11 and 14) have normal chewing mandibles and well-developed maxillae with two distinct lobes. In *Diplocotes familiaris* both structures are somewhat reduced, and in *Ectrephes formicarum* the mandible is narrow and scoop-like (Fig. 13) and the maxilla is highly reduced (Fig. 12). Reduction of mouthparts and feeding by ants is a common feature in other symphiles. According to Donisthorpe (1927), *Artemeles* (Staphylinidae) elicits food from worker ants by tapping with its antennae, but can survive on ant larvae and dead insects as well. Park (1964) described an individual of *Adranes lecontei* Brendel being fed regurgitated food by one worker

while two more ants were licking its trichomes.

Since many species of Ptinidae, including almost all of the inquilines, are wingless in both sexes, the means of dispersal in these insects is difficult to explain. A clue may be found in observations made on certain clavigerine Pselaphidae, which are also wingless. *Adranes lecontei* Brendel is known to ride the gaster of worker ants and has been observed to be carried in this manner for as long as ninety minutes (Park, 1964). *Claviger testaceus* Preyssler may attach itself to winged females and males of its host, and Donisthorpe (1927) noted that two specimens of *Claviger longicornis* Müller frequently sat for hours on the gaster of an *Acanthomyops fuliginosus* queen. It is quite possible, then, that a number of myrmecophilous insects may be transported to new nests by queen ants.

The small number of available host records makes it impossible at present to determine the extent to which particular ptinids are restricted to one species or one group of ants. In the New World, *Gnostus* is known only from *Crematogaster* nests and *Fabrasia* is associated only with *Camponotus*, but in Australia the situation is more complex. Many of the Australian forms are associated with species of *Iridomyrmex*, but several have been found in *Crematogaster* and *Rhytidoponera* nests. Seven different ptinids have been taken in the nests of *Iridomyrmex conifer* Forel, and some have been associated with as many as three ant species. *Iridomyrmex conifer* occurs in the dry southwestern part of Australia, and it builds large, conical mounds of twigs and leaves. Most of the Australian ant hosts are ground nesting, while *Camponotus* and *Crematogaster* in the New World usually build nests off the ground in rotten wood, twigs, and vines.

#### Origin of Myrmecophily

According to Crowson (1955), the Ptinidae have probably evolved from an anobiid-like ancestor resembling the genus *Hedobia*,

with the loss of the wood-boring habit being the most important factor involved in the divergence of the group. He considers the ptinid genus *Xylodes* to be intermediate between *Hedobia* and a primitive *Ptinus*, such as *P. palliatus*. Assuming that there was a shift from xylophagy to general scavenging, the ancestral forms may have first fed on rotten wood mixed with excrement and insect remains. Some extant species have retained this habit, as noted above. Two independent trends must then have taken place: (1) the movement away from the arboreal or woody habitat, and (2) the increased utilization of animal by-products, including stored food, feces, and carrion. It is not surprising that many species came to inhabit the nests of birds, mammals, and insects, since the greatest accumulations of suitable food items would be found in these habitats. Also, the Ptinidae have become particularly successful in arid regions where nests of various kinds provide one of the few habitats in which sufficient moisture is available for the completion of the life cycle. Howe (1959) stresses the fact that ptinids require "drinking" water, which would be present in nests in the form of urine, moist excrement, honey, or other fluids. As mentioned above, the species which invaded warehouses and mills were probably first associated with rats and mice. From these general nest scavengers evolved the depredaters, such as *Ptinus californicus* and *P. sexpunctatus*, and the myrmecophiles.

The invasion of the nests of social insects, such as ants, presents a problem to the potential inquiline, who must overcome the strong defenses of the colony. Unlike the myrmecophilous Staphylinidae, the slow-moving ptinids certainly have never been active predators, and the first species to penetrate ant colonies were probably indifferently tolerated forms or synoeketes, in the terminology of Wasmann (1898). *Ptinus subpilosus* is a living species which may be a synoekete, since it lacks trichomes or other symphilic features but appears to

have invaded successfully the nests of *Acanthomyops* in Europe. These secretive forms may be able to survive in the nest by occupying abandoned chambers or by feigning death when disturbed (letisimulation). The latter type of behavior, which has been discussed by Park (1964) for the Pselaphidae, may have been very important in the initial adjustment to the ant society. It is likely that beetles exhibiting letisimulation would be ignored by worker ants or possibly carried off with the debris. It is also possible that certain structural features of the Ptinidae have preadapted them for myrmecophilous existence. All ptinids are relatively small and compact beetles with a heavy cuticle. The head is declined and the prosternum shortened, so that the mouthparts and antennae may be hidden beneath the body. If a beetle were to be attacked, the compact form and thick cuticle might provide sufficient protection, but this would not be necessary for survival if enough of the population avoided encounters with the ants. Once this initial adjustment was made, the inquiline would be provided with a compatible environment (especially in arid regions), an abundant food supply, and the protection of the colony. Selection would favor the subsequent evolution of features either that would improve the defenses of the inquiline or allow it to become integrated into the ant society as a protected symphile.

There is little doubt that in several groups, such as the Ptinidae, Paussidae, and Pselaphidae, the evolution of true symphily has been associated with the development of glandular structures, such as trichomes, but the functions of these glands and the steps leading to their development are far from being clearly understood. It is known that ants may imbibe the secretions and that insects possessing trichomes are often protected and fed by ants, but the relationships between symphiles and their hosts have never been studied in detail. Unlike aphids and coccids, these insects are not tended in groups

outside the nest, nor do they supply a significant amount of nutriment to the colony. Symphiles are known to occur in small numbers throughout the active portions of the nest and they appear to be accepted as part of the colony. It may be argued that any "foreign" insect producing secretions which stimulate the ants to feed would be devoured rather than protected, but several factors may prevent this. First, it has been assumed that the initial invaders have penetrated the nest in the manner discussed above and have thus taken on the colony odor. Second, most of these symphiles resemble ants and some of them, at least, exhibit antlike behavior. Third, the aggressive behavior of a foraging or defending worker is unlike that of an ant within the nest, where a common activity is the exchange of regurgitated food or secretions (trophallaxis). If a myrmecophile elicits no defensive response from the ants, and if trophallactic exchange is a common pattern among individuals within the nest, it is conceivable that the development of attractive secretions by an inquiline might lead directly to a situation in which the insect is not only protected but also fed by the ants.

In the preceding discussion it is assumed that trichomes developed in beetles which already had invaded successfully the nests of ants. It is also possible that these glands were a necessary prerequisite to the invasion of nests. Cazier and Mortenson (1965) suggest that in the scarabaeid beetle *Cremastocheilus* trichomes may serve to attract ants to the beetles which are then carried into the nest as items of food. A third alternative is that trichomes evolved independently and serve no necessary function in myrmecophily. We think that the occurrence of these structures in so many unrelated myrmecophiles makes this last suggestion improbable.

As mentioned above, myrmecophily in the Ptinidae probably originated several times. *Myrmecoptinus butteli*, a winged species associated with *Crematogaster* in

the forests of Southeast Asia, is the least modified of the inquilines and may have evolved recently from non-myrmecophilous forms. We have suggested (Lawrence and Reichardt, 1966a) that the two New World genera, *Gnostus* and *Fabrasia*, evolved directly and independently from early *Ptinus*-like ancestors. The species in both groups are highly modified symphiles, but they have retained their wings and are associated with arboreal or wood-nesting ants in the American tropics. The South African *Diplocotidus* and the Australian ectrephines are all wingless, and most of them occur with ground-nesting ants in open, arid or semi-arid regions. These two groups may have evolved from ancestors which had already left the ancestral forest habitat and were associated with ground debris or mammal burrows in dry areas. *Diplocotidus formicola* is a true symphile, judging from the observations of Wasmann and Brauns (1925), but it has not evolved some of the more obvious antennal and pronotal modifications found in the Australian forms. The ectrephines are the most diverse and numerous of the myrmecophilous ptinids, but they have almost certainly evolved from one or possibly two related forms; all are probably symphiles, but the degree of structural modification varies considerably.

Only six species of myrmecophilous ptinids occur in the Neotropical region, while 35 species are known from Australia. Furthermore, the New World fauna consists of three closely related species in each of the two genera, while the Australian fauna is so diverse that the species were formerly placed in 14 genera. Certainly the habitat diversity of South America exceeds that of Australia, and the ant faunas of the two areas are comparable. The following factors are likely to have been responsible. First, the Ptinidae in general seem to be more successful in arid and semi-arid regions than in humid, tropical ones, and most of the Australian ectrephines inhabit the drier parts of the continent. Second,

the Australian inquilines are all wingless (which may be related to water conservation in dry areas), while the New World species are winged. The lack of wings will obviously reduce the rate of gene exchange between populations. If, as suggested above, the wingless myrmecophile must attach itself to a new queen, then the probability of outbreeding will be very low. Finally, the Australian ant fauna contains a large number of ground-nesting species, such as *Iridomyrmex conifer*, which build mounds and have relatively large and permanent colonies. The South American ants, on the whole, have smaller and less permanent colonies. These *Iridomyrmex* nests provide a suitable environment for the build-up of inquiline populations, which, because of difficulties of dispersal, may be isolated from other such populations for long periods of time. Such conditions would favor the evolution of a diverse myrmecophilous fauna.

### Evolutionary Trends

In examining the various modifications of myrmecophilous ptinids, we may distinguish between those unique to inquilines and those found in other Ptinidae as well. The former group would include: elongation of clypeus and labrum, reduction of mouthparts, enlargement, flattening, and fusion of antennal segments, formation of glandular structures on antennae, pronotum, elytra, and hind legs, changes in shape of tibiae, and loss or extreme reduction of hairs and scales over most of the body surface. The following would fall into the latter group: reduction of eyes, declination of head, formation of deep antennal fossae, loss of antennal segments, formation of grooves and pits on pronotum, loss of hindwing, reduction or loss of scutellum and elytral humeri, reduction of metasternum, and lateral movement and change in shape of hind coxae.

The loss of the hindwings (with the correlated changes in the elytra, scutellum, and metasternum) occurs in various Ptin-

idae, including *Mezium*, *Gibbium*, *Niptus*, and *Trigonogenius*, while some of the myrmecophiles have fully developed wings (*Gnostus* and *Fabrasia*). Since most of the wingless ptinids occur in drier areas or in stored products, it is possible that the loss of wings is associated with water conservation.

Changes in the shape of the clypeus and labrum are unique to the myrmecophilous species, and may serve to protect the mouthparts. In some of the highly modified forms, such as *Ectrephes*, the concave inner surface of the labrum forms with the hollowed and elongate mandibles a tube which may be used for feeding on liquids supplied by the ants. In these same forms, the chewing surface of the mandible is absent and the maxillae are reduced.

Modifications of the legs of these inquilines probably represent three different kinds of adaptations. In *Gnostus*, the tibiae are broad and compressed and may serve as protective shields; very similar structures occur in the paussid genera *Homopterus* and *Cerapterus*. The tibiae of *Ectrephes formicarum* and certain other ectrephines are somewhat bent and angulate; these might be used to cling to ants. The hind tibiae and femora of *Fabrasia* are peculiarly enlarged and bear tufts of yellow hairs; these are probably glandular structures serving the same function as trichomes.

The types and possible functions of pronotal and antennal trichomes have been discussed above. Several different types of glandular systems have evolved in this group, but the diversity is not nearly as great as in the Paussidae (see Darlington, 1950). Perhaps the first structures were small isolated glands scattered on the body surface. A consolidation of these small glands gave rise to more complicated organs, such as trichomes, and to various accessory grooves and pits for the collection of fluid. The fusion of antennal segments would serve to consolidate glandular material and form a storage vesicle as well.

The evolution of antennal types in the

Ptinidae is similar in many ways to that occurring in the Paussidae, and a number of convergences can be seen in the two groups. *Protopaussus* has simple antennae like those of *Diplocotes familiaris*, while *Homopterus*, *Cerapterus*, and their relatives have the flattened type of antennae found in *D. laticornis*. *Lebioderus* and *Pentaplatarthrus* have flattened antennae with a reduced number of segments, and in *Ceratoderus* and *Platyhopalopsis* further fusion and reduction can be seen; this series finds a parallel in *Diplocotes kingi*, *Ectrephes clavatus*, and *E. pascoei* among the ptinids. The club-like antenna found in *E. formicarum* and the genus *Gnostus* is similar to that of some *Paussus*.

## CATALOGUE OF THE MYRMECOPHILOUS PTINIDAE

### *Myrmecoptinus* Wasmann

*Myrmecoptinus* Wasmann, 1916: 206-207. Type species, by monotypy, *Myrmecoptinus butteli* Wasmann.

*Included species: 1.*

### *Myrmecoptinus butteli* Wasmann

*Myrmecoptinus butteli* Wasmann, 1916: 207, pl. 4, fig. 20.

*Distribution:* SUMATRA (Soengei, Bانبان).

*Host: Crematogaster butteli* Forel.

### *Diplocotidus* Peringuey

*Diplocotidus* Peringuey, 1899: 245. Type species, by monotypy, *Diplocotidus formicola* Peringuey.

*Included species: 1.*

### *Diplocotidus formicola* Peringuey

*Diplocotidus formicola* Peringuey, 1899: 245-246, pl. 7, figs. 13, 13a; Wasmann and Brauns, 1925: 112-113.

*Distribution:* UNION OF SOUTH AFRICA (Prince Albert; Willowmore; Lady-smith; Kimberley).

*Hosts: Acantholepis capensis* Mayr; *Anoplolepis custodiens* (F. Smith); *Anoplolepis steingroeveri* (Forel).



**Gnostus Westwood**

*Gnostus* Westwood, 1855: 90–92; Lawrence and Reichardt, 1966a: 32–34. Type species, by monotypy, *Gnostus formicicola* Westwood.

*Included species:* 3.

**Gnostus formicicola Westwood**

*Gnostus formicicola* Westwood, 1855: 92, pl. 8, figs. 1–21; Lawrence and Reichardt, 1966a: 34, fig. 4.

*Distribution:* BOLIVIA: LA PAZ (Mapiri); BRAZIL: PARÁ (Santarém; Villa Nova); AMAZONAS (São Paulo de Olivença); MATO GROSSO (Utiariti).

*Hosts:* *Crematogaster victima* F. Smith; *Crematogaster* sp. (near *brasiliensis* Mayr).

**Gnostus floridanus Blatchley**

*Gnostus floridanus* Blatchley, 1930: 111–112, fig. 1; Lawrence and Reichardt, 1966a: 37, figs. 1, 2, 5, 13, 14.

*Distribution:* BAHAMAS (Clifton Point, New Providence); FLORIDA (Dunedin; Plantation Key).

*Hosts:* *Crematogaster ashmeadi* Mayr; *Crematogaster sanguinea lucayana* Wheeler.

**Gnostus meinerti Wasmann**

*Gnostus meinerti* Wasmann, 1894: 121, 216; Lawrence and Reichardt, 1966a: 35, fig. 3.

*Distribution:* PANAMA (Barro Colorado Is.; Erwin Is.; Gatun Lake); VENEZUELA: CARABOBO (Trincheras, near Valencia).

*Host:* *Crematogaster limata dextella* Santschi.

**Fabrasia Martinez and Viana**

*Fabia* Martinez and Viana, 1964: 8, not Dana, 1851. Type species, by original designation, *Fabia alvarengai* Martinez and Viana.

*Fabrasia* Martinez and Viana, 1965: 18; Lawrence and Reichardt, 1966a: 37–40.

*Included species:* 3.

**Fabrasia alvarengai (Martinez and Viana)**

*Fabia alvarengai* Martinez and Viana, 1964: 9, figs. 1–3.

*Fabrasia alvarengai* (Martinez and Viana), 1965: 18; Lawrence and Reichardt, 1966a: 41.

*Distribution:* BRAZIL: RIO GRANDE DO NORTE (Natal).

*Host:* Unknown.

**Fabrasia borgmeieri Lawrence and Reichardt**

*Fabrasia borgmeieri* Lawrence and Reichardt, 1966a: 41–42, figs. 6–7.

*Distribution:* BRAZIL: GOIÁS (Campinas); MINAS GERAIS (Poços de Caldas).

*Host:* *Camponotus (Myrmothrix) renggeri* Emery; *Camponotus (Myrmobrachys) senex* (F. Smith).

**Fabrasia wheeleri Lawrence and Reichardt**

*Fabrasia wheeleri* Lawrence and Reichardt, 1966a: 42–44, figs. 8–12.

*Distribution:* COLOMBIA: MAGDALENA (Sevilla); MEXICO: OAXACA (6.3 mi. W Tehuantepec).

*Host:* *Camponotus (Myrmothrix) bugnioni* Forel.

**Diplocotes Westwood**

*Diplocotes* Westwood, 1869: 317. Type species, by monotypy, *Diplocotes howittanus* Westwood. *Diphobia* Olliff, 1886: 837–838. Type species, by monotypy, *Diphobia familiaris* Olliff. NEW SYNONYMY.

*Paussoptinus* Lea, 1905: 381. Type species, by monotypy, *Paussoptinus laticornis* Lea. NEW SYNONYMY.

*Decemplocotes* Mjöberg, 1916: 2; Lea, 1917: 146 (proposed synonymy with *Diplocotes*). Type species, by present designation, *Diplocotes strigicollis* Lea.

*Mesectrephes* Mjöberg, 1916: 3. Type species, by monotypy, *Ectrephes kingi* Westwood. NEW SYNONYMY.

*Bitrephes* Oke, 1926: 291; Oke, 1928: 27. Type species, by monotypy, *Bitrephes cuneiformis* Oke. NEW SYNONYMY.

*Falsocktrephes* Pic, 1929: 35. Type species, by monotypy, *Ectrephes kingi* Westwood. NEW SYNONYMY.

*Included species:* 19.

**Diplocotes apicalis (Oke),  
NEW COMBINATION**

*Polyplocotes apicalis* Oke, 1928: 26.

*Distribution:* AUSTRALIA: VICTORIA (Hattah).

*Host:* *Iridomyrmex* sp.

***Diplocotes armicollis* Lea**

*Diplocotes armicollis* Lea, 1910: 219–220, figs. 25–26.

*Distribution:* AUSTRALIA: SOUTH AUSTRALIA (Adelaide).

*Host:* Unknown. Collected under bark with ants.

***Diplocotes brevipennis* (Pic)**

*Pausoptinus brevipennis* Pic, 1909: 215; Lea, 1910: 223.

*Decemplocotes brevipennis*, – Mjöberg, 1916: 6, fig. 6.

*Diplocotes brevipennis*, – Lea, 1917: 146.

*Diplocotes decemarticulatus* Lea, 1910: 220–221, fig. 57; Lea, 1917: 146 (syn.).

*Distribution:* AUSTRALIA: WESTERN AUSTRALIA (Geraldton; Moora).

*Host:* Unknown.

***Diplocotes carinaticeps* (Lea),****NEW COMBINATION**

*Polyplocotes carinaticeps* Lea, 1919: 254–255, pl. 25, fig. 39; Zeck, 1920: 246, pl. 19, fig. 3; Oke, 1928: 27.

*Distribution:* AUSTRALIA: VICTORIA (Hattah); WESTERN AUSTRALIA (Swan River).

*Hosts:* *Crematogaster laeviceps* F. Smith; *Iridomyrmex conifer* Forel.

***Diplocotes cuneiformis* (Oke),****NEW COMBINATION**

*Bitrephes cuneiformis* Oke, 1926: 291; Oke, 1928: 27–28.

*Distribution:* AUSTRALIA: VICTORIA (Lake Hattah).

*Host:* *Iridomyrmex rufoniger* (Lowne).

***Diplocotes familiaris* (Olliff),****NEW COMBINATION**

*Diphobia familiaris* Olliff, 1886: 838; Lea, 1905: 381; Lea, 1910: 223.

*Diplocotes niger* Poll, 1886: 238; Blackburn, 1892: 300 (syn.).

*Distribution:* AUSTRALIA: SOUTH AUSTRALIA (Adelaide); VICTORIA (Kiata).

*Hosts:* *Iridomyrmex nitidus* Mayr; *Iridomyrmex nitidiceps* Andre; *Rhytidoponera metallica* (F. Smith).

***Diplocotes foveatus* (Lea),****NEW COMBINATION**

*Diphobia foveata* Lea, 1917: 154–155.

*Distribution:* AUSTRALIA: QUEENSLAND (Townsville).

*Host:* Unknown.

***Diplocotes foveicollis* Olliff**

*Diplocotes foveicollis* Olliff, 1886: 839–840; Lea, 1910: 219; Lea, 1917: 149; Lea, 1919: 257; Clark, 1921: 103.

*Distribution:* AUSTRALIA: NEW SOUTH WALES; SOUTH AUSTRALIA (Lucindale); WESTERN AUSTRALIA (Serpentine River; Perth; Swan River).

*Host:* *Iridomyrmex conifer* Forel.

***Diplocotes howittanus* Westwood**

*Diplocotes howittanus* Westwood, 1869: 317; Westwood, 1874: 103, pl. 3, fig. 6; Lea, 1910: 219; Oke, 1928: 26.

*Distribution:* AUSTRALIA: SOUTH AUSTRALIA (Gawler, Adelaide); VICTORIA (Grampians).

*Host:* Unknown. Collected under bark with ants.

***Diplocotes intricatus* (Lea),****NEW COMBINATION**

*Diphobia intricata* Lea, 1917: 155–156.

*Distribution:* AUSTRALIA: QUEENSLAND (Stewart River).

*Hosts:* *Crematogaster* sp.; *Iridomyrmex* sp.

***Diplocotes kingi* (Westwood),****NEW COMBINATION**

*Ectrephes kingi* Westwood, 1869: 316; Westwood, 1874: 104, pl. 3, fig. 2; Lea, 1910: 222; Lea, 1917: 147.

*Mesectrephes kingi*, – Mjöberg, 1916: 3.

*Falsoectrephes kingi*, – Pic, 1929: 35.

*Distribution:* AUSTRALIA: WESTERN AUSTRALIA (Swan River; Mullewa).

*Host:* *Iridomyrmex* sp.

***Diplocotes laticornis* (Lea),****NEW COMBINATION**

*Pausoptinus laticornis* Lea, 1905: 382–383, pl. 28, fig. 7; Lea, 1917: 147; Tillyard, 1926: 215, pl. 16, fig. 14.

*Distribution:* AUSTRALIA: SOUTH AUSTRALIA (Mindarie; Murat Bay; Murray Bridge; Port Lincoln); VICTORIA (Birchip; Bendigo; Sea Lake).

*Hosts:* *Crematogaster laeviceps* F. Smith; *Iridomyrmex nitidus* Mayr; *Iridomyrmex* spp.

***Diplocotes longicornis* (Lea),  
NEW COMBINATION**

*Diphobia longicornis* Lea, 1919: 256, pl. 25, fig. 40; Zeck, 1920: 245, pl. 19, fig. 4; Clark, 1921: 103.

*Distribution:* AUSTRALIA: WESTERN AUSTRALIA (Victoria Park; Swan River).

*Hosts:* *Iridomyrmex conifer* Forel; *Iridomyrmex* sp.

***Diplocotes metallicus* (Lea),  
NEW COMBINATION**

*Diphobia metallica* Lea, 1917: 155.

*Distribution:* AUSTRALIA: QUEENSLAND (Stewart River).

*Host:* *Iridomyrmex* sp.

***Diplocotes minutus* Oke**

*Diplocotes minuta* Oke, 1928: 26.

*Distribution:* AUSTRALIA: VICTORIA (Bendigo).

*Host:* *Rhytidoponera* sp.

***Diplocotes myrmecophilus* (Lea),  
NEW COMBINATION**

*Diphobia myrmecophila* Lea, 1917: 153–154.

*Distribution:* AUSTRALIA: NORTHERN TERRITORY (Darwin).

*Hosts:* *Oecophylla smaragdina* (Fabricius), *Rhytidoponera hilli* Crawley.

***Diplocotes pilosus* (Mjöberg),  
NEW COMBINATION**

*Polyplacotes pilosus* Mjöberg, 1916: 11–12, fig. 3.

*Distribution:* AUSTRALIA: WESTERN AUSTRALIA (Noonkanbah, Kimberley District).

*Host:* Unknown.

***Diplocotes similis* (Oke),  
NEW COMBINATION**

*Polyplacotes similis* Oke, 1928: 27.

*Distribution:* AUSTRALIA: VICTORIA (Bendigo; Inglewood).

*Host:* *Crematogaster laeviceps* F. Smith.

***Diplocotes strigicollis* Lea**

*Diplocotes strigicollis* Lea, 1910: 221; Lea, 1917: 150.

*Decemplocotes strigicollis*, – Mjöberg, 1916: 2.

*Distribution:* AUSTRALIA: SOUTH AUSTRALIA (Adelaide; Port Lincoln).

*Host:* *Iridomyrmex* sp.

***Polyplacotes* Westwood**

*Polyplacotes* Westwood, 1869: 316. Type species, by present designation, *Polyplacotes longicollis* Westwood.

*Hexaplocotes* Lea, 1906: 224. Type species, by monotypy, *Hexaplocotes sulcifrons* Lea. NEW SYNONYMY.

*Leaptinus* Mjöberg, 1916: 3; Lea, 1917: 146 (proposed synonymy with *Paussoptinus*). Type species, by monotypy, *Paussoptinus dolichognathus* Lea. NEW SYNONYMY.

*Paussoceros* Mjöberg, 1916: 13. Type species, by monotypy, *Paussoceros antennalis* Mjöberg. NEW SYNONYMY.

*Included species:* 11.

***Polyplacotes antennalis* (Mjöberg),  
NEW COMBINATION**

*Paussoceros antennalis* Mjöberg, 1916: 13–14, fig. 4.

*Distribution:* AUSTRALIA: WESTERN AUSTRALIA (Derby, Kimberley District).

*Host:* Unknown. Collected under bark.

***Polyplacotes castaneus* Lea**

*Polyplacotes castaneus* Lea, 1912: 75.

*Distribution:* AUSTRALIA: WESTERN AUSTRALIA (Northwestern Australia).

*Host:* Unknown.

***Polyplacotes cremastogastri* (Lea),  
NEW COMBINATION**

*Paussoceros cremastogastri* Lea, 1917: 153.

*Distribution:* AUSTRALIA: WESTERN AUSTRALIA (Derby).

*Host:* *Crematogaster* sp.

***Polyplocotes dolichognathus* (Lea),  
NEW COMBINATION**

*Pausoptinus dolichognathus* Lea, 1912: 76; Lea, 1917: 146.

*Leaptinus dolichognathus*, - Mjöberg, 1916: 3.

**Distribution:** AUSTRALIA: SOUTH AUSTRALIA (Killalpanima, Central Australia).

**Host:** Unknown.

***Polyplocotes longicollis* Westwood**

*Polyplocotes longicollis* Westwood, 1869: 316; Westwood, 1874: 103, pl. 3, fig. 4; Lea, 1910: 219; Lea, 1917: 147.

?*Polyplocotes nigropiceus* Pic, 1903: 183.

**Distribution:** AUSTRALIA: WESTERN AUSTRALIA (Cue; Swan River; Sorrento Beach, Perth District).

**Host:** *Iridomyrmex* sp.

***Polyplocotes longipes* Lea**

*Polyplocotes longipes* Lea, 1917: 152-153.

**Distribution:** AUSTRALIA: WESTERN AUSTRALIA (Derby).

**Host:** *Crematogaster* sp.

***Polyplocotes nitidus* Westwood**

*Polyplocotes nitidus* Westwood, 1869: 316; Westwood, 1874: 103, pl. 3, fig. 5; Lea, 1910: 219.

**Distribution:** AUSTRALIA: WESTERN AUSTRALIA (Swan River).

**Host:** Unknown. Collected with ants.

***Polyplocotes ovipennis* Lea**

*Polyplocotes ovipennis* Lea, 1914: 256-257.

**Distribution:** AUSTRALIA: SOUTH AUSTRALIA (Lake Callabonna, Central Australia).

**Host:** Unknown.

***Polyplocotes perforatus* Lea**

*Polyplocotes perforatus* Lea, 1917: 150-151, pl. 12, figs. 7-8.

**Distribution:** AUSTRALIA: WESTERN AUSTRALIA (Beverley).

**Host:** Unknown. Collected in nests of ants.

***Polyplocotes scabricollis* Lea**

*Polyplocotes scabricollis* Lea, 1917: 151-152.

**Distribution:** AUSTRALIA: NORTH-EASTERN TERRITORY (Stapleton).

**Host:** Unknown. Collected in ant nest.

***Polyplocotes sulcifrons* (Lea),  
NEW COMBINATION**

*Hexaplocotes sulcifrons* Lea, 1906: 224-225, pl. 18, fig. 8; Lea, 1917: 150; Clark, 1921: 104; Tillyard, 1926: 215, pl. 16, fig. 13.

**Distribution:** AUSTRALIA: WESTERN AUSTRALIA (Beverley; Newcastle; Perth).

**Host:** *Iridomyrmex conifer* Forel.

***Ectrephes* Pascoe**

*Ectrephes* Pascoe, 1866: xvi; Westwood, 1869: 315.

Type species, by monotypy, *Ectrephes formicarum* Pascoe.

*Anapestus* King, 1866: 317; Westwood, 1869: 315 (proposed synonymy with *Ectrephes*). Type species, by monotypy, *Anapestus kreusleri* King (= *Ectrephes formicarum* Pascoe).

*Monectrephes* Mjöberg, 1916: 3; Lea, 1917: 145 (proposed synonymy with *Ectrephes*). Type species, by present designation, *Ectrephes pascoei* Westwood.

*Pseudectrephes* Pic, 1929: 35 (proposed as a subgenus of *Ectrephes*); Schenkling, 1935: 4 (raised to rank of genus). Type species, by monotypy, *Ectrephes clavatus* Mjöberg.

**Included species:** 3.

***Ectrephes clavatus* Mjöberg**

*Ectrephes clavatus* Mjöberg, 1916: 14, fig. 5.

*Ectrephes* (*Pseudectrephes*) *clavatus*, -Pic, 1929: 35.

**Distribution:** AUSTRALIA: WESTERN AUSTRALIA (Swan River).

**Host:** *Iridomyrmex nitidus* Mayr.

***Ectrephes formicarum* Pascoe**

*Ectrephes formicarum* Pascoe, 1866: xvi-xvii; Westwood, 1869: 315; Westwood, 1874: 104, pl. 3, fig. 1; Lea, 1910: 222; Lea, 1919: 256, pl. 25, figs. 41-42; Zeck, 1920: 246, pl. 19, fig. 1; Clark, 1921: 103; Tillyard, 1926: 215, pl. 16, fig. 15.

*Anapestus kreusleri* King, 1866: 317, pl. 16; Westwood, 1869: 315 (syn.).

**Distribution:** AUSTRALIA: SOUTH AUSTRALIA; WESTERN AUSTRALIA (Jandakot; Perth; Swan River).

**Hosts:** *Iridomyrmex conifer* Forel; *Rhytidoponera metallica* (F. Smith).

**Ectrephes pascoei** Westwood

*Ectrephes pascoei* Westwood, 1869: 315–316;  
Westwood, 1874: 104, pl. 3, fig. 3.

*Monectrephes pascoei*, – Mjöberg, 1916: 3.

**Distribution:** AUSTRALIA: WESTERN AUSTRALIA (Swan River).

**Host:** Unknown.

**Enasiba** Olliff

*Enasiba* Olliff, 1886: 838–839. Type species, by monotypy, *Enasiba tristis* Olliff.

**Included species:** 2.

**Enasiba microcera** Clark

*Enasiba microcera* Clark, 1923: 44–46.

**Distribution:** AUSTRALIA: WESTERN AUSTRALIA (Bunbury; Busselton).

**Host:** *Iridomyrmex conifer* Forel.

**Enasiba tristis** Olliff

*Enasiba tristis* Olliff, 1886: 839; Lea, 1919: 254, pl. 25, figs. 37–38; Zeck, 1920: 245, pl. 19, fig. 2; Clark, 1921: 103; Clark, 1923: 46; Tillyard, 1926: 215, pl. 16, fig. 12.

**Distribution:** AUSTRALIA: WESTERN AUSTRALIA (King George's Sound; Perth; Swan River).

**Host:** *Iridomyrmex conifer* Forel.

## LIST OF ANT HOST SPECIES AND ASSOCIATED INQUILINES

## Formicidae

## Ponerinae

## Ectatommini

<i>Rhytidoponera hilli</i> Crawley .....	<i>D. myrmecophilus</i> (Lea)
<i>R. metallica</i> (F. Smith) .....	<i>D. familiaris</i> (Olliff)
	<i>E. formicarum</i> Pascoe
<i>Rhytidoponera</i> sp. ....	<i>D. minutus</i> Oke

## Myrmicinae

## Crematogastrini

<i>Crematogaster ashmeadi</i> Mayr .....	<i>G. floridanus</i> Blatchley
<i>C. butteli</i> Forel .....	<i>M. butteli</i> Wasmann
<i>C. laeviceps</i> F. Smith .....	<i>D. carinaticeps</i> (Lea)
	<i>D. laticornis</i> (Lea)
	<i>D. similis</i> (Oke)
<i>C. limata dextella</i> Santschi .....	<i>G. meinerti</i> Wasmann
<i>C. sanguinea lucayana</i> Wheeler .....	<i>G. floridanus</i> Blatchley
<i>C. victima</i> F. Smith .....	<i>G. formicicola</i> Westwood
<i>Crematogaster</i> sp. ....	<i>G. formicicola</i> Westwood
	<i>D. intricatus</i> (Lea)
	<i>P. crematogastris</i> (Lea)
	<i>P. longipes</i> Lea

## Dolichoderinae

## Tapinomini

<i>Iridomyrmex conifer</i> Forel .....	<i>D. carinaticeps</i> (Lea)
	<i>D. foveicollis</i> Olliff
	<i>D. longicornis</i> (Lea)
	<i>P. sulcifrons</i> (Lea)
	<i>E. formicarum</i> Pascoe
	<i>E. microcera</i> Clark
	<i>E. tristis</i> Olliff
<i>I. nitidiceps</i> Andre .....	<i>D. familiaris</i> (Olliff)

<i>I. nitidus</i> Mayr .....	<i>D. familiaris</i> (Olliff)
	<i>D. laticornis</i> (Lea)
	<i>E. clavatus</i> Mjöberg
<i>I. rufoniger</i> (Lowne) .....	<i>D. cuneiformis</i> (Oke)
<i>Iridomyrmex</i> sp. ....	<i>D. apicalis</i> (Oke)
	<i>D. intricatus</i> (Lea)
	<i>D. kingi</i> (Westwood)
	<i>D. laticornis</i> (Lea)
	<i>D. longicornis</i> (Lea)
	<i>D. metallicus</i> (Lea)
	<i>D. strigicollis</i> Lea
	<i>P. longicollis</i> Westwood
Formicinae	
Plagiolepidini	
<i>Acantholepis capensis</i> Mayr .....	<i>D. formicola</i> Peringuey
<i>Anoplolepis custodiens</i> (F. Smith) .....	<i>D. formicola</i> Peringuey
<i>A. steingroeveri</i> (Forel) .....	<i>D. formicola</i> Peringuey
Oecophyllini	
<i>Oecophylla smaragdina</i> (Fabricius) .....	<i>D. myrmecophilus</i> (Lea)
Camponotini	
<i>Camponotus</i> ( <i>Myrmobrachys</i> ) <i>senex</i> (F. Smith) .....	<i>F. borgmeieri</i> Lawrence and Reichardt
<i>C. (Myrmothrix) bugnioni</i> Forel .....	<i>F. wheeleri</i> Lawrence and Reichardt
<i>C. (Myrmothrix) renggeri</i> Emery .....	<i>F. borgmeieri</i> Lawrence and Reichardt

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## LITERATURE CITED

- ANDREWS, R. 1968. Notes on the biology of two Central American *Ptinus* (Coleoptera: Ptinidae) with a description of a new species. *Psyche* **74** (3): 191-202.
- BLACKBURN, T. 1892. Notes on Australian Coleoptera with descriptions of new species. *Proc. Linn. Soc. New South Wales* **7** (2): 283-300.
- BLATCHLEY, W. S. 1930. On a family of Coleoptera new to the fauna of North America with description of one new species (Gnostidae). *Ent. News* **41**: 108-112.
- BROWN, W. J. 1959. *Niptus* Boield. and allied genera in North America (Coleoptera: Ptinidae). *Canad. Ent.* **91**: 627-633.
- CAZIER, M. A., AND M. A. MORTENSON. 1965. Bionomical observations on myrmecophilous beetles of the genus *Cremastocheilus* (Coleoptera: Scarabaeidae). *Jour. Kansas Ent. Soc.* **38** (1): 19-44.
- CHAPIN, E. A. 1965. The genera of the Chilodorini (Coleoptera, Coccinellidae). *Bull. Mus. Comp. Zool.* **133**: 227-271.
- CLARK, J. 1921. Notes on Western Australian ant-nest beetles. *Jour. Proc. Roy. Soc. Western Australia* **6** (2): 97-104.
- . 1923. A new myrmecophilous beetle. *Jour. Proc. Roy. Soc. Western Australia* **9** (1): 44-46.
- COSTA LIMA, A. DA. 1962. Micro-coleoptero representante da nova subfamilia Plaumanniolinae (Col., Ptinidae). *Rev. Bras. Biol.* **22** (4): 413-418.
- CROWSON, R. A. 1955. The Natural Classification of the Families of Coleoptera. London, Lloyd, 187 pp.
- . 1962. Observations on Coleoptera in Scottish oak woods. *Glasgow Nat.* **18**: 177-195.
- DANA, J. D. 1851. *Conspectus Crustaceorum quae in orbis terrarum circumnavigatione, Carolo Wilkes e classe Reipublicae Foederatae duce, lexit et descripsit.* [Part.] *Proc. Acad. Nat. Sci. Philadelphia* **5**: 247-254, 267-272.
- DARLINGTON, P. J., JR. 1950. Paussid beetles. *Trans. Amer. Ent. Soc.* **76**: 47-142.
- DONISTHORPE, H. 1927. *The Guests of British Ants. Their Habits and Life Histories.* London, Routledge, 244 pp.
- FALL, H. C. 1901. List of the Coleoptera of Southern California. . . . San Francisco, Calif. Acad. Sci., 282 pp.
- . 1905. Revision of the Ptinidae of boreal America. *Trans. Amer. Ent. Soc.* **31**: 97-296, pl. 7.
- FORBES, W. T. M. 1926. The wing folding patterns of the Coleoptera. *Jour. New York Ent. Soc.* **34**: 42-68, 91-139, pls. 7-18.
- GEMMINGER, M., AND E. VON HAROLD. 1968. *Catalogus Coleopterorum hujusque descriptorum synonymicus et systematicus.* Tom. II. Dytiscidae . . . Scaphidiidae. Monaco, Gumm, pp. 425-752.
- HINTON, H. E. 1941. The Ptinidae of economic importance. *Bull. Ent. Res.* **31**: 331-381.
- HOWE, R. W. 1959. Studies on beetles of the family Ptinidae. XVII.—Conclusions and additional remarks. *Bull. Ent. Res.* **50**: 287-326.
- JANSENS, E. 1949. Sur la massue antennaire de *Paussus* Linné et genres voisins. *Inst. Roy. Sci. Nat. Belg.* **25** (22): 1-19.
- KING, R. L. 1866. Description of *Anapestus kreusleri*: a species of coleopterous insect inhabiting ants' nests in South Australia. *Trans. Ent. Soc. New South Wales* **1** (5): 316-318, pl. 16.
- LAWRENCE, J. F. 1967. Delimitation of the genus *Ceracis* (Coleoptera: Ciidae) with a revision of North American species. *Bull. Mus. Comp. Zool.* **136** (6): 91-144.
- , AND H. REICHARDT. 1966a. Revision of the genera *Gnostus* and *Fabrasia* (Coleoptera: Ptinidae). *Psyche* **73**: 30-45.
- , ———. 1966b. The systematic position of *Plaumanniola* Costa Lima (Coleoptera: Scydmaenidae). *Coleopt. Bull.* **20**: 39-42.
- LEA, A. M. 1905. On *Nepharis* and other ant's nest beetles taken by Mr. J. C. Gondie at Birchip. *Proc. Roy. Soc. Victoria (n.s.)* **17** (2): 371-385.
- . 1906. Descriptions of new species of Australian Coleoptera. Part VIII. *Proc. Linn. Soc. New South Wales* **31** (2): 195-227, pl. 18.
- . 1910. Australian and Tasmanian Coleoptera inhabiting or resorting to the nests of ants, bees, and termites. *Proc. Roy. Soc. Victoria (n.s.)* **23** (1): 116-230, pls. 25-27.
- . 1912. Australian and Tasmanian Coleoptera inhabiting or resorting to the nests of ants, bees, and termites. Supplement. *Proc. Roy. Soc. Victoria (n.s.)* **25** (1): 31-78, pl. 2.
- . 1914. Notes on some miscellaneous Coleoptera, with descriptions of new species. *Trans. Proc. Roy. Soc. South Australia* **38**: 249-344, pl. 16.
- . 1917. Notes on some miscellaneous Coleoptera, with descriptions of new species. Part III. *Trans. Proc. Roy. Soc. South Australia* **41**: 121-322, pls. 12-15.
- . 1919. Notes on some miscellaneous Coleoptera, with descriptions of new species. Part V. *Trans. Proc. Roy. Soc. South Australia* **43**: 166-261, pls. 25-27.
- LINSLEY, E. G. 1944. Natural sources, habitats, and reservoirs of insects associated with stored food products. *Hilgardia* **16**: 187-224.

- , AND J. W. MACSWAIN. 1941. The bio-nomics of *Ptinus californicus*, a depredator in the nests of bees. *Bull. So. Calif. Acad. Sci.* **40** (3): 126-137, pls. 11-14.
- MARTINEZ, A., AND M. J. VIANA. 1964. Una nueva subfamilia de Coleopteros (Ptinidae; Fabiinae). *Neotropica* **10**: 7-14.
- , ———. 1965. Un caso de homonimia en Ptinidae (Coleoptera). *Neotropica* **11**: 18.
- MJÖBERG, E. 1916. Results of Dr. E. Mjöberg's Swedish scientific expeditions to Australia 1910-1913. 8. Ptinidae. *Ark. Zool.* **10** (6): 1-15.
- MOC, Y. C. 1938. Morphologische und histologische Studien über Paussidendrusen. *Zool. Jahrb. (Abt. Anat.)* **64**: 287-346.
- OKE, C. 1926. Two entomologists in the Mallee. *Vict. Nat.* **42**: 279-294.
- . 1928. Notes on Australian Coleoptera, with descriptions of new species. Part i. *Proc. Linn. Soc. New South Wales* **53** (2): 1-30.
- OLLIFF, S. A. 1886. Remarks on Australian Ptinidae and descriptions of new genera and species. *Proc. Linn. Soc. New South Wales* **10**: 833-840.
- PARK, O. 1942. A study in Neotropical Pselaphidae. *Northwestern Univ. Stud. Biol. Sci. Med.* **1**: 403 pp.
- . 1964. Observations upon the behavior of myrmecophilous pselaphid beetles. *Pedobiologia* **4**: 129-137.
- PASCOE, F. P. 1866. [Note.] *Trans. Ent. Soc. London*, ser. 3, vol. 5, *Jour. Proc.*, 1866: xv-xvii.
- PERINGUEY, L. 1899. Fifth contribution to the South African coleopterous fauna. *Ann. South African Mus.* **1** (2): 240-330, pls. 6-7.
- PIC, M. 1903. Diagnoses generiques et spécifiques de divers Coléoptères exotiques. *L'Échange* **19**: 182-183.
- . 1909. Ptinidae. *In*: W. Michaelsen and R. Hartmeyer, eds., *Die Fauna Südwest-Australiens* **2** (13): 215.
- . 1912. Ptinidae. *In*: W. Junk and S. Schenkling, eds., *Coleopterorum catalogus* **10** (41): 1-46.
- . 1929. Über Wasmann's Ectrephidae. *Wien. Ent. Zeit.* **46** (1): 34-35.
- POLL, J. VAN DE. 1886. Description of a new gnostid. *Notes Leyden Mus.* **8**: 238.
- REDELLE, J. R. 1966. A checklist of the cave fauna of Texas. II. Insecta. *Texas Jour. Sci.* **18** (1): 25-56.
- REICHENSBERGER, A. 1948. Die Paussiden Afrikas. *Abhandl. Senckenberg. Naturforsch. Ges.* No. 479, 32 pp.
- REITTER, E. 1911. *Fauna Germanica. Die Käfer des deutschen Reiches.* Band III. Stuttgart, Lutz, 436 pp.
- SCHENKLING, S. 1935. Ectrephidae. *In*: W. Junk and S. Schenkling, eds., *Coleopterorum catalogus* **10** (141): 3-4.
- SHARP, D., AND F. MUIR. 1912. The comparative anatomy of the male genital tube in Coleoptera. *Trans. Ent. Soc. London* **1912**: 477-642, pls. 42-78.
- STICKNEY, F. S. 1923. The head-capsule of Coleoptera. *Univ. Illinois Biol. Monogr.* **8** (1): 1-104.
- TILLYARD, R. J. 1926. *The Insects of Australia and New Zealand.* Sydney, Angus and Robertson, 560 pp.
- TULLOCH, G. S. 1960. Torre-Bueno's Glossary of Entomology—Supplement A. Merrick, New York, Brooklyn Ent. Soc., 36 pp.
- WASMANX, E. 1894. *Kritisches Verzeichniss der myrmekophilen und termitophilen Arthropoden.* Berlin, Dames, 231 pp.
- . 1898. Die Gaste der Ameisen und Termiten. *Illustr. Zeit. Ent.* **3**: 145-149, 161-164, 179-181, 195-197, 209-211, 225-227, 243-246.
- . 1916. *Wissenschaftliche Ergebnisse einer Forschungsreise nach Ostindien. . . . V. Termitophile und myrmecophile Coleopteren. . . .* *Zool. Jahrb.* **39**: 169-210, pls. 4-5.
- . 1920. Die Gastpflege der Ameisen, ihre biologischen und philosophischen Probleme. *J. Schaxel's Abhandlungen zur theoretischen Biologie*, Heft 4, xvii + 176 pp.
- . 1928. Ptinidae aus Sumatra und Java (Coleopt.). (275 Beitrag zur Kenntnis der Myrmecophilen.) *Ent. Mitt.* **17**: 242-244.
- , AND H. BRAUNS. 1925. New genera and species of South African myrmecophilous and termitophilous beetles. *So. Afr. Nat. Hist.* **5**: 101-118, pls. 9-10.
- WESTWOOD, J. O. 1855. Description of a new genus of coleopterous insects inhabiting the interior of ants' nests, in Brazil. *Trans. Ent. Soc. London*, Ser. 2, **3**: 90-94, pl. 8.
- . 1869. Remarks on the genus *Ectrephes*, and descriptions of new exotic Coleoptera. *Trans. Ent. Soc. London* **1869**: 315-320.
- . 1874. *Thesaurus Entomologicus Oxoniensis. . . .* Oxford, Clarendon, 205 pp.
- WHEELER, W. M. 1928. *The Social Insects. Their Origin and Evolution.* New York, Harcourt, Brace, 378 pp.
- ZECK, E. H. 1920. Myrmecophilous Coleoptera. *Austral. Zool.* **1** (8): 245-247, pl. 19.

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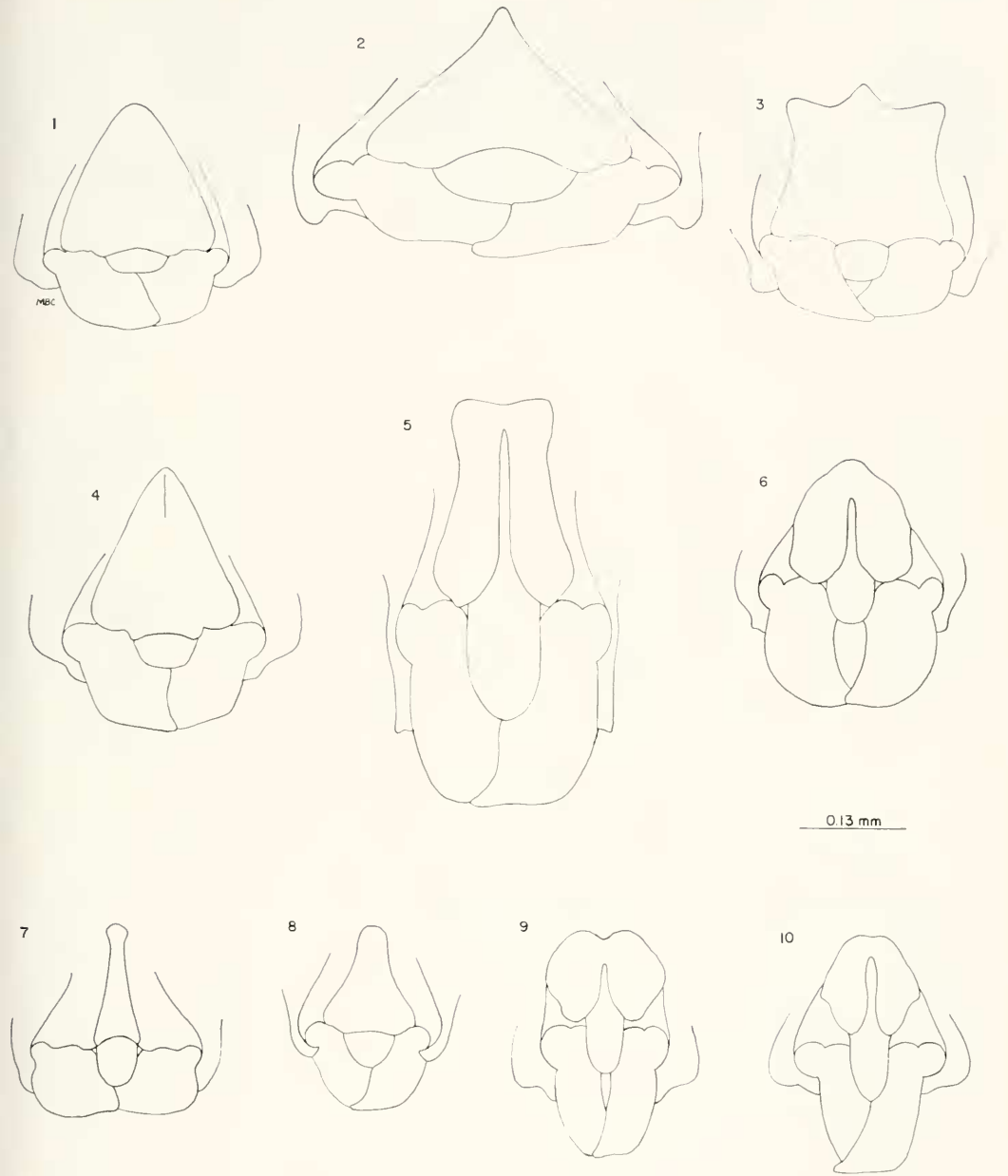


Plate 1. Figs. 1-10. Facial region (clypeus, labrum, and mandibles) of various Ptinidae. Fig. 1. *Diplocotes familiaris* (Olliff). Fig. 2. *Ptinus californicus* Pic. Fig. 3. *Diplocotidus formicola* Peringuey. Fig. 4. *Diplocotes laticornis* (Leo). Fig. 5. *Enasiba tristis* Olliff. Fig. 6. *Polyplocotes longicollis* Westwood. Fig. 7. *Diplocotes carinataiceps* (Oke). Fig. 8. *Diplocotes kingi* (Westwood). Fig. 9. *Ectrephes pascoei* Westwood. Fig. 10. *Ectrephes formicarum* Poscoe.

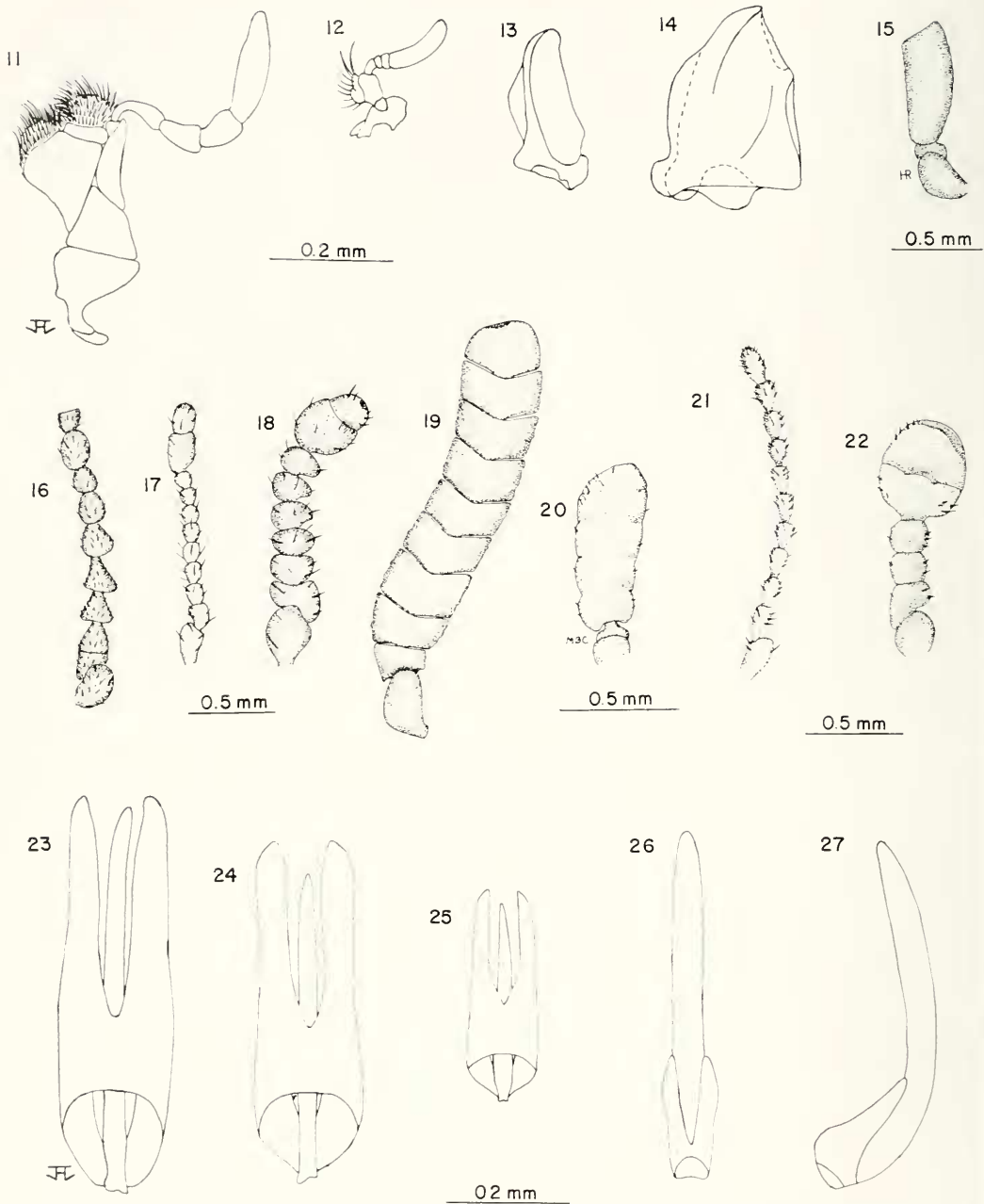


Plate 2. Figs. 11, 12. Maxillo. Fig. 11. *Pinus fur* Linnaeus. Fig. 12. *Ectrephes formicarum* Pascoe. Figs. 13, 14. Mandible. Fig. 13. *Ectrephes formicarum* Pascoe. Fig. 14. *Pinus fur* Linnaeus. Figs. 15-22. Antenna. Fig. 15. *Ectrephes formicarum* Pascoe. Fig. 16. *Enasiba tristis* Olliff. Fig. 17. *Diplocotes foveicollis* Olliff. Fig. 18. *Polyplacotes longicollis* Westwood. Fig. 19. *Diplocotes laticornis* (Lea). Fig. 20. *Ectrephes pascoei* Westwood. Fig. 21. *Diplocotes familiaris* (Olliff). Fig. 22. *Polyplacotes sulcifrons* (Lea). Figs. 23-28. Aedeagus (with basal piece removed). Fig. 23. *Diplocotes familiaris* (Olliff). Fig. 24. *Diplocotes laticornis* (Lea). Fig. 25. *Ectrephes formicarum* Pascoe. Fig. 26. *Diplocotidus formicola* Peringuey, ventral. Fig. 27. Same, lateral.

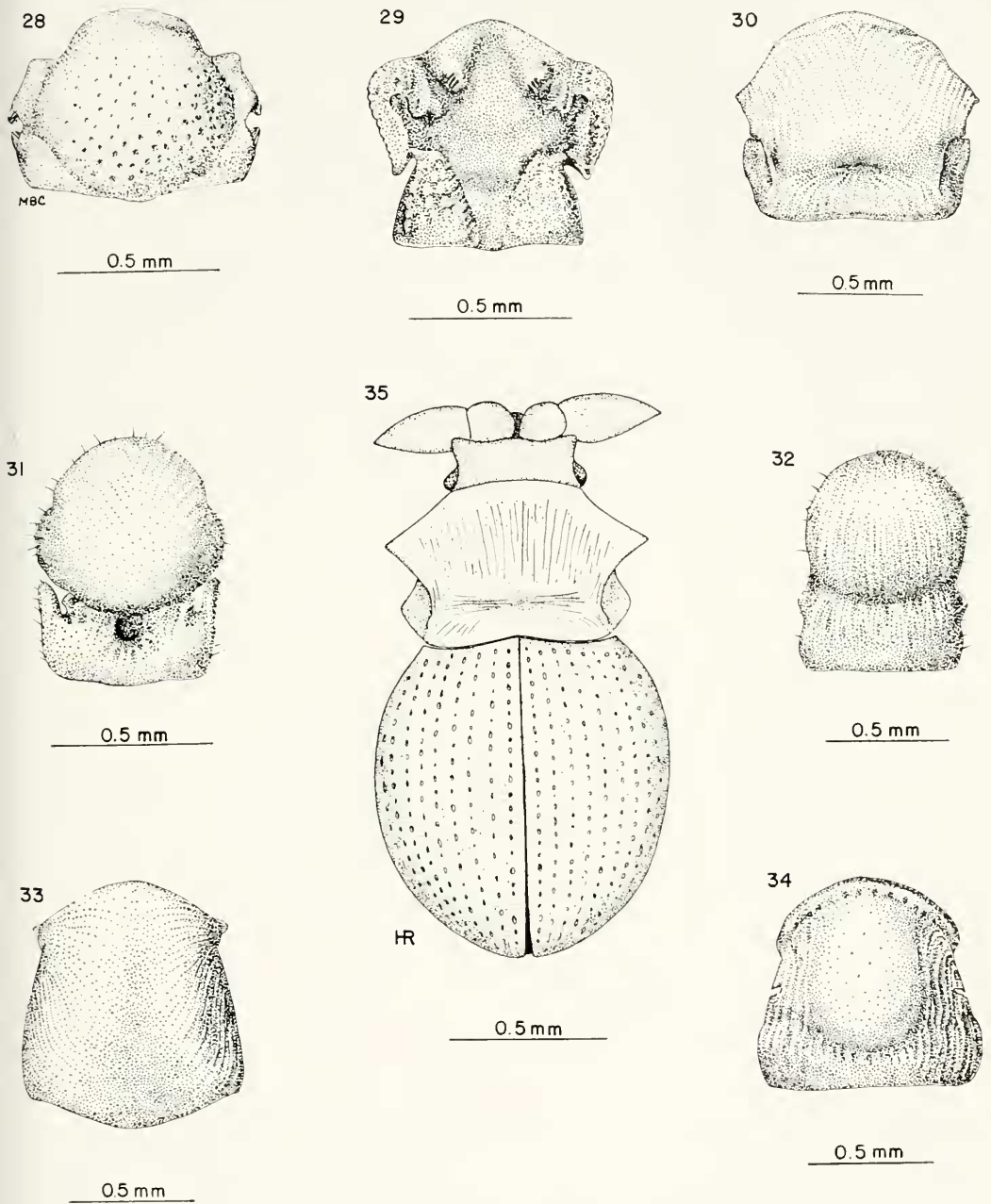


Plate 3. Figs. 28-34. Pronotum of various myrmecophilous Ptinidae. Fig. 28. *Etrephes farmicarum* Pascoe. Fig. 29. *Diplocotidus formicola* Peringuey. Fig. 30. *Diplocotes laticornis* (Lea). Fig. 31. *Diplocotes longicornis* (Lea). Fig. 32. *Diplocotes familiaris* (Olliff). Fig. 33. *Polyplacotes perforatus* Lea. Fig. 34. *Polyplacotes longicallis* Westwood. Fig. 35. *Diplocotes cuneiformis* (Oke).